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Seasonal Changes in the Amphipod Fauna of 'Microciona prolifera' (Ellis and Solander) (Porifera: Demospongia) and Associated Sponges in a Shallow Salt-Marsh Creek

Charleston Coll., SC

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16. ABSTRACT

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Seasonal Changes in the Amphipod Fauna of *Microciona prolifera* (Ellis and Solander) (Porifera: Demospongia) and Associated Sponges in a Shallow Salt-Marsh Creek[1]

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ABSTRACT: Between September 1976 and August 1978, samples of four species of sponge, *Microciona prolifera* (Ellis and Solander), *Haliclona loosanoffi* Hartman, *Lissodendoryx isodictyalis* (Carter) and *Halichondria bowerbanki* Burton, were collected from subtidal shell debris in a North Edisto River, South Carolina saltmarsh creek and associated amphipods identified. Dominant spongicolous amphipods were *Colomastix halichondriae* Bousfield, *Leucothoe spinicarpa* (Abildgaard), *Corophium simile* Shoemaker, *Corophium acherusicum* Costa, *Lembos* cf. *L. websteri* Bate and *Melita appendiculata* (Say). Densities of amphipods in *Microciona prolifera* and *Halichondria bowerbanki* usually exceeded those in *Lissodendoryx isodictyalis* and *Haliclona loosanoffi*. Seasonal changes in amphipod dominance were however approximately the same in all sponge species. Winter dominance by *Corophium* spp., and on occasion *Lembos* spp., is followed by spring dominance by *Melita appendiculata* and summer dominance by *Colomastix halichondriae*. Harsher winter conditions in 1976–77 apparently resulted in more reduced populations of various sponge species as well as *Colomastix halichondriae* and *Leucothoe spinicarpa* when compared with the following winter. With some exceptions during the winter, amphipod density in *Microciona prolifera* generally decreased as sponge size increased. The range of gammarid amphipod densities in *Microciona prolifera* was 128–724 individuals per 5 g (40.3 cm^3) of sponge.

Introduction

Sponges have long been known to harbor a diverse assemblage of organisms that have parasitic, commensal, or mutualistic relationships with their host. Certain groups of animals can be particularly common in this living habitat, e.g., nematodes, polychaetes, pycnogonids, copepods, amphipods, alpheid shrimp, brachyuran crabs, ophiuroids, hydroids, and ectoprocts. In areas where sponges are common these associated organisms may represent a significant portion of the benthic fauna, especially where the substrate (such as shell debris) is unstable or unsuitable for most infaunal species. Patches of such substrates are frequently found in estuaries. Despite the prevalence of shell debris in estuaries, the sponge-associated organisms in these patches have been little studied, with the notable exception of studies by Pearse (1932, 1950), Arndt (1933), Bacescu (1971), and Frith (1976).

This study analyzes amphipods living in subtidal sponges found on oyster shell debris in a South Carolina saltmarsh creek. Amphipods, common and occasionally dominant sponge associates (Arndt 1933; Frith 1976), have been shown (like other benthic taxa) to be sensitive to numerous characteristics of their substrate (Meadows 1964; Hargrave 1970; Biernbaum 1979). It is to be expected that they would also show sensitivity toward various characteristics of a live substrate, such characteristics perhaps differing between different species of sponge. Arndt (1933) has reported that of

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300 species of crustaceans known to be associated with sponges as of that date, 53 were amphipods. He emphasized that the size of the sponge is of importance in determining what taxa may be present; larger sponges contain more taxa and larger bodied taxa, e.g., decapods (Pearse 1932, 1950). Depth of occurrence and sponge morphology are also important factors (Arndt 1933; Pearse 1932, 1950; Frith 1976).

There are many amphipod species that are particularly characteristic of marine or freshwater sponges, several of them restricted largely to a living substrate, e.g., sponge, ascidian, or alcyonarian. Families Lysianassidae, Melitidae, and Corophiidae contain several such species in addition to those most commonly reported as sponge associates: *Tritaeta gibbosa* (Bate), *Colomastix pusilla* Grube, and *Leucothoe spinicarpa* (Abildgaard) (Pearse 1932; Arndt 1933; Bacescu and Mayer 1960; Connes 1967; Bacescu 1971; Ortiz 1975). Amphipods found associated with sponges may represent a variety of living habits, e.g., epifaunal tube-dwellers (*Corophium, Erichthonius, Lembos*), epifaunal crawlers or nestlers (*Melita, Gammarus, Tritaeta, Stenothoe, Pleusymtes*, caprellids), or inquilines (*Colomastix, Leucothoe*) (Arndt 1933; Biernbaum 1979). Occasionally, adhering sediment may harbor burrowers (*Paraphoxus, Monoculodes*) or infaunal tube-dwellers (*Ampelisca*). Studies by Frith (1976, 1977) have indicated that amphipods may utilize either tactile or chemosensory capabilities in locating sponge colonies.

Epifaunal organisms, such as sponges, are important members of coastal ecosystems. One of the most distinctive characteristics of sponges is their importance as living substrates for a wide variety of organisms. This investigation will add to the small amount of information known about the inhabitants of this common substrate.

Materials and Methods

The sampling location is a small creek located in a North Edisto River saltmarsh approximately 30 km southwest of Charleston, South Carolina. This saltmarsh creek passes through the center of the approximately 370 ha marsh and drains into Leadenwah Creek, which empties into the North Edisto River (Fig. 1). As is true of many such creeks, patches of oyster shell debris alternate with soft, muddy sediment. This subtidal shell debris has a relatively rich epifauna consisting of sponges, hydroids, anthozoans, barnacles, ectoprocts, nudibranchs, amphipods, crabs, and alpheid shrimp. A single creek location in the approximate center of the marsh was used for this study. Depths at this site ranged to 4 m, recorded salinities were 20–34‰, and recorded temperatures 5–27 °C. Fig. 2 indicates seasonal water temperature changes recorded at the Bears Bluff Environmental Protection Agency Field Station approximately 3 km upriver from the sampling location. Studies of the North Edisto River have indicated that, because of little freshwater inflow, the system has only minor variations in salinity, both along the river's length and seasonally (Calder, et al. 1977). Seasonal salinity fluctuations were therefore judged to be less important in this study than temperature fluctuations.

Between September 1976 and August 1978, sponge samples were taken at approximately 4–6-week intervals, 1–10 colonies (median = 5) collected each time for each species found. SCUBA was utilized to place the sponges in a jar while still on the bottom to prevent loss of any sponge associates. Between September 1976 and July 1977, sponges of each observed species were placed in a separate jar for each species. Between August 1977 and August 1978, each individual sponge was placed in a separate jar. So that the data of the second year are comparable to the first, the total mass of sponge and number of amphipods are determined for each sponge species on each sampling date and calculations based on these values. Sponges were preserved in 5% seawater-formalin and macerated in the laboratory; all fauna retained by a 300 μm screen were saved and amphipods identified. Sponge material was dried at 100 °C for 12 h and dry weight recorded. Since spongicolous species are undoubtedly more sensitive to volume rather than mass of sponge, several individuals of each sponge species were collected and their densities determined by volume displacement and

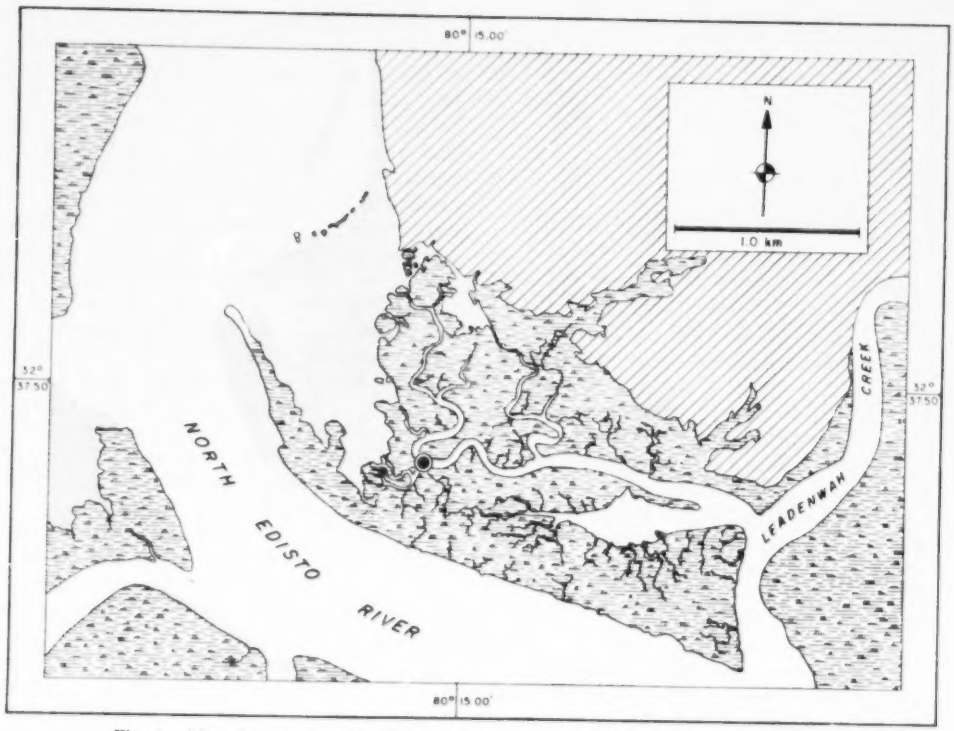

Fig. 1. Map showing sampling area. Sampling location is indicated by a circled dot.

drying at 100 °C for 12 h. Note that this is not a measurement of the density of sponge tissue since the volume measurement includes water adhering to and contained within the sponge. However, it does permit conversion of sponge colony mass to volume.

Results

Dominant sponge species in this sampling area are *Microciona prolifera* (Ellis and Solander), *Haliclona loosanoffi* Hartman, *Lissodendoryx isodictyalis* (Carter), *Halichondria bowerbanki* Burton and *Cliona* spp. (boring sponge). The first four species were analyzed for sponge inhabitants. *Microciona prolifera* and *Halichondria bowerbanki* are both highly branched, upright species, while *Haliclona loosanoffi* and *Lissodendoryx isodictyalis* are generally rough-surfaced encrusting species that sometimes reach thicknesses as great as 5–6 cm. The only non-boring sponge found through all four seasons at observable sizes was *Microciona prolifera*, which reached maximum growth in late summer and early fall. *Halichondria bowerbanki* was presumably killed by the long winter conditions of 1976–77 (see Fig. 2) and was not seen after January 1977. *Lissodendoryx isodictyalis* was also found to be a cold-sensitive species. It was greatly reduced in abundance after January 1977, then recovered by July 1977, but reduced once more by September 1977. *Haliclona loosanoffi* was more tolerant of winter conditions, reaching maximum abundance in late fall and surviving the winters as small patches.

The winters of 1976–77 and 1977–78 were two of the most severe winters on record in the eastern United States (Moyer 1977; Anonymous 1978). During the previous 17 years the mean number of days having temperatures below 8.5 °C in Charleston harbor was 18 ± 17.6 (SD) (Farmer and Whitaker

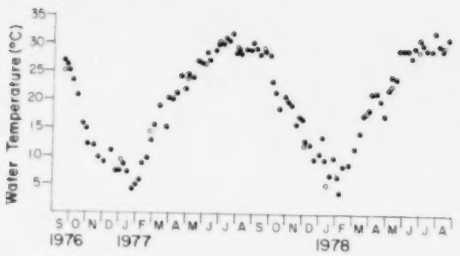

Fig. 2. Temperatures in the Leadenwah marsh area. Closed circles indicate the mean of the maximum and minimum temperatures recorded during a one-week period at the Bears Bluff EPA dock. Open circles are temperatures recorded at the sampling location.

1978). The winters of 1976–77 and 1977–78 had totals of 48 and 45 d respectively when temperatures in Charleston harbor were below 8.5 °C (Farmer and Whitaker 1978). When comparing the two winters, the winter of 1976–77 had more days below 7 °C (26 compared to 13) and below 6 °C (13 compared to 4) (Whitaker, pers. commun.). The winter of 1976–77 clearly had a more severe effect on sponge abundance in the present study than did the winter of 1977–78. Reference to Fig. 2 reveals that temperatures below 10 °C in the study area lasted somewhat longer in the winter of 1976–77. This longer winter severely reduced a rich fall 1976 sponge fauna, with *Haliclona loosanoffi* being the last to die-back. Evidence of wide-spread disintegration of colonies of this species was seen when diving on February 27, 1977. *Microciona prolifera* recovered most rapidly the following summer, followed by moderate recovery of *Lissodendoryx isodictyalis*, which was replaced by *Haliclona loosanoffi* by December 1977. It was not until June 1978, that the sponge fauna approached the richness of the fauna seen prior to the winter of 1976–77.

These seasonal changes are similar to those found elsewhere by other investigators. Wells, et al. (1964) also found that *Microciona prolifera* was common throughout the year in North Carolina, reaching maximum growth in late fall. *Haliclona loosanoffi* was common in North Carolina in winter. Minimum sizes occurred in summer and large colonies were found by December, as was true in this study. In contrast to North Carolina observations, Hartman (1958) reported that New England colonies of *Haliclona loosanoffi* died during the winter, as occurred in this study during the harsh winter of 1976–77. Hartman found that mild winters had little effect on *Halichondria bowerbanki*, while harsh winters could kill all colonies. This apparently did happen in the present study, since this species was not observed after January 1977. The late summer density maximum observed in the present study for *Lissodendoryx isodictyalis*, a primarily tropical and subtropical species, was similar to that found in North Carolina (Wells, et al. 1964). Evidence of overgrowth of *Lissodendoryx isodictyalis* by *Haliclona loosanoffi* in the fall of 1976 was seen in the study area, similar to observations made in North Carolina (Wells, et al. 1964).

Since *Mirociona prolifera* was the only sponge species sampled throughout the entire two year period, most conclusions concerning seasonal changes of spongicolous amphipods uses those collected from this species. Amphipod faunas of other sponge species are then compared to that found in *Microciona prolifera*. In addition to amphipods, other macrofaunal taxa were abundant in sponges. Frequently exceeding amphipods in numbers were polychaetes (belonging to several families), those in the family Spionidae being especially numerous. *Lissodendoryx isodictyalis* and *Haliclona loosanoffi* frequently had dense spionid concentrations associated with large mats of mud tubes in and on the sponge.

Table 1 records the densities of all amphipod species in 5 g of sponge. A 5 g-colony of ramous *Microciona prolifera* collected in this study was approximately 18 cm wide and had a dense growth of upright lobes approximately 14 cm in length. Dominant spongicolous amphipod species are *Colomastix halichondriae* Bousfield, *Leucothoe spinicarpa* (Abildgaard), *Corophium simile* Shoemaker, *Corophium acherusicum* Costa, *Lembos* cf *L. websteri* Bate, and *Melita appendiculata* (Say). *Colomastix halichondriae* is a characteristic sponge symbiont (similar to *Colomastix pusilla*) and *Leucothoe spinicarpa* is a common symbiont of a variety of hosts, especially sponges and ascidians, as well as occasionally found

TABLE 1. Occurrence of amphipod species in four sponge species. Recorded as range of density in 5 g of sponge and mean density when present (parentheses).

	Microciona prolifera	*Lissodendoryx isodictyalis*	*Haliclona loosanoffi*	*Halichondria bowerbanki*
Ampelisca abdita Mills[a]	0–1.8 (1.8)	0–4.9 (4.9)	0	0
A. vadorum Mills[a]	0	0	0–0.4 (0.4)	0
Batea catharinensis Muller	0–0.5 (0.5)	0	0	0
Colomastix halichondriae Bousfield	18.4–446.2 (114.0)	0–92.5 (56.2)	1.0–85.4 (45.6)	303.0–1,563.8 (668.6)
Corophium acherusicum Costa	0–130.5 (35.8)	0–3.0 (3.0)	0–10.5 (4.6)	1.0–44.9 (17.4)
C. simile Shoemaker	7.8–116.3 (48.7)	0.4–4.2 (2.2)	3.9–108.3 (27.9)	4.7–29.7 (20.7)
Erichthonius brasiliensis Dana	0–8.2 (3.2)	0	0–2.7 (1.3)	0–3.3 (3.0)
Gammarus mucronatus Say	0–1.1 (1.1)	0	0	0
Gitanopsis sp.	0–25.2 (5.4)	0.2–0.4 (0.3)	0–6.2 (1.5)	0.3–9.5 (4.1)
Lembos smithi Holmes	0	0–4.4 (4.4)	0	0
L. unicornis Bynum and Fox	0–1.9 (1.9)	0–4.4 (4.4)	0	0–8.4 (8.4)
L. cf *L. websteri* Bate[b]	0–139.2 (35.9)	0–24.1 (9.5)	2.3–572.9 (95.9)	8.4 –119.0 (62.2)
Leucothoe spinicarpa (Abildgaard)	1.0–55.1 (26.4)	0–190.6 (95.1)	0–45.8 (20.5)	27.8–87.9 (56.1)
Melita appendiculata (Say)	4.7–459.0 (88.7)	4.4–25.8 (14.8)	0–50.8 (11.2)	15.8–94.9 (46.3)
M. nitida Smith	0–19.5 (9.9)	0–1.2 (0.6)	0–33.6 (7.3)	0–1.3 (0.8)
Monoculodes sp.	0	0–0.2 (0.2)	0	0
Paraphoxus spinosus Holmes	0–2.4 (1.4)	0–0.8 (0.6)	0–2.1 (0.7)	0.3–5.2 (2.1)
Pleusymtes sp.	0–32.4 (10.3)	0	0–52.1 (52.1)	0
Stenothoe sp.	0–0.8 (0.6)	0	0	0
Caprella equilibra Say	0–24.3 (5.6)	0	0	0–5.6 (3.4)
Paracaprella tenuis Mayer	0–159.1 (18.5)	0.2–0.8 (0.5)	0–131.1 (27.5)	0–2.5 (2.4)

[a] Infaunal species occurring in adhering sediment.
[b] Fox (1978) states that a new species closely resembling *L. websteri* occurs in South Carolina.

free-living (Bousfield 1973; Ortiz 1975). The other species can be found on a variety of substrates. *Corophium simile* commonly builds tubes on the base of sponges or tunicates as well as on other surfaces (Bousfield 1973).

Caprellids, especially *Paracaprella tenuis* Mayer, were frequently abundant. As noted by Arndt (1933), however, their numbers were less determined by amount of sponge than by the amount of hydroid or bryozoan growth on the sponge.

Figs. 3–8 show seasonal changes in densities of dominant amphipod species and all gammarids in *Microciona prolifera*. One must be cautious when evaluating the data due to large inter-colony density variations demonstrated by the multiple samples collected the second year. Unfortunately, possible depletion of the sponge fauna precluded taking numerous colonies at any one time. *Colomastix halichondriae* (Fig. 3) shows a population maximum in the summer of 1977, following and preceding winter depressions. The summer of 1978, however, did not reveal a significant population increase. *Melita appendiculata* (Fig. 4) shows density maxima in both springs, with the population peak in spring 1977 especially pronounced due to the presence of large numbers of recently released juveniles. Using the Student's t-test, the density of *Melita appendiculata* in May 1978 is significantly greater ($p < 0.05$) than densities found the preceding January and the following August. As was seen with *Colomastix halichondriae*, *Leucothoe spinicarpa* (Fig. 5) shows a winter population depression, with the harshest winter associated with the greatest depression. *Lembos* spp. (Fig. 6) had winter and spring maxima each year, with the largest population density associated with the harshest winter. *Corophium* spp. (Fig. 7) showed maximum densities in late winter, especially in the harsh winter of 1976–77. High densities during this winter were largely due to the presence of large numbers of *Corophium acherusicum*, which was found in far lower densities the following winter.

Fig. 9 shows seasonal changes in amphipod dominance patterns in *Microciona prolifera*. During the winter the fauna is dominated by *Corophium* spp. This is followed by spring dominance by *Melita appendiculata* (less pronounced the second year),

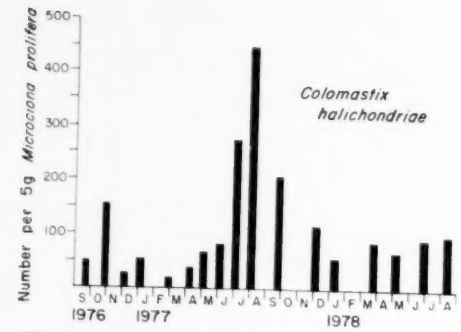

Fig. 3. Density of *Colomastix halichondriae* in *Microciona prolifera*.

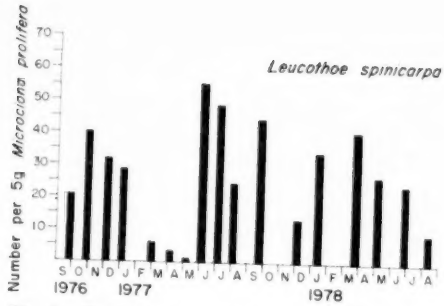

Fig. 5. Density of *Leucothoe spinicarpa* in *Microciona prolifera*.

closely followed by summer dominance by *Colomastix halichondriae*. It is evident that, although *Colomastix halichondriae* does not show a significant increase in density in summer 1978 (Fig. 3), it does dominate the summer fauna. *Lembos* spp. is important in late fall, when *Melita appendiculata* once again becomes an important faunal component.

There are major similarities as well as differences between the amphipod fauna of *Microciona prolifera* and that of other sponges. Table 2 records densities of amphipods in these other species. The same major seasonal trends in species densities and faunal dominance observed in *Microciona prolifera* are seen in *Lissodendoryx isodictyalis* and *Halichondria bowerbanki*, even though absolute density values may differ. Although *Haliclona loosanoffi* has similar trends for *Colomastix halichondriae*, *Melita appendiculata*, and *Lembos* spp., trends for *Leucothoe spinicarpa* and *Corophium* spp. are quite different from those seen in the other sponge species.

Densities of amphipods in *Lissodendoryx isodictyalis* are considerably below those found in *Microciona prolifera*, with the exception of summer densities of *Leucothoe spinicarpa*. When compared with dominance patterns in *Microciona prolifera*, *Lissodendoryx isodictyalis* shows greater importance of *Lembos* spp. in winter and greater importance of *Leucothoe spinicarpa* and less importance of *Colomastix halichondriae* in summer. Student's t-tests were done to compare the densities and percent of fauna of *Colomastix halichondriae* and *Leucothoe spinicarpa* in *Microciona prolifera* and *Lissodendoryx isodictyalis* collected in August 1977. Densities of both *Colomastix halichondriae* and *Leucothoe spinicarpa* are significantly different in the

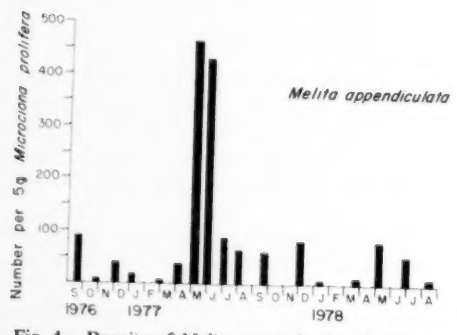

Fig. 4. Density of *Melita appendiculata* in *Microciona prolifera*.

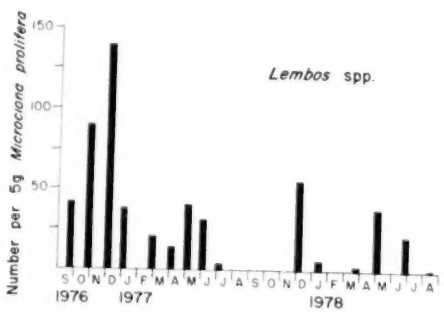

Fig. 6. Density of *Lembos* spp. in *Microciona prolifera*.

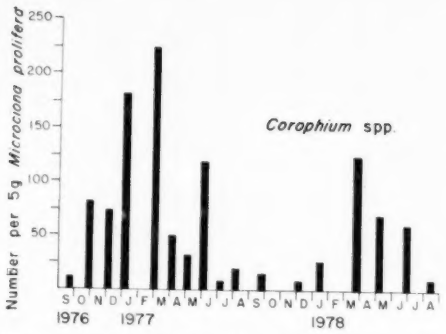

Fig. 7. Density of *Corophium* spp. in *Microciona prolifera*.

two sponge species ($p < 0.05$ and $p < 0.01$ respectively). Faunal proportions of these two species were also significantly different ($p < 0.01$; $p < 0.001$). However, as considered above, if sponge quantity is a significant factor affecting amphipod abundance, sponge volume is probably more important than mass. With *Microciona prolifera* having a mean density of 0.124 g per cm³ (s = 0.009) and *Lissodendoryx isodictyalis* having a mean density of 0.086 g per cm³ (s = 0.006), comparisons of densities based on sponge volume rather than mass makes low densities in *Lissodendoryx isodictyalis* even more apparent. If, for example, one compares the amphipod densities of August 1977 samples, based on the approximate volume represented by 5 g of *Microciona prolifera* (40 cm³), *Microciona prolifera* has a total gammarid density of 565 per 40 cm³ and *Lissodendoryx isodictyalis* a total gammarid density of 210 per 40 cm³. These values compare to values of 569 per 5 g and 306 per 5 g respectively.

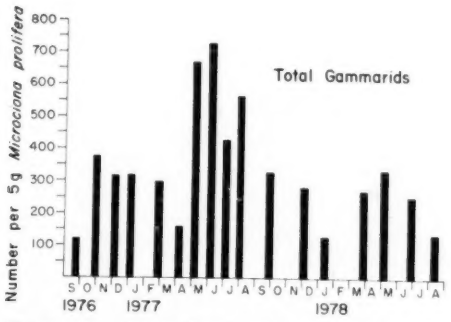

Fig. 8. Density of all gammarid amphipods in *Microciona prolifera*.

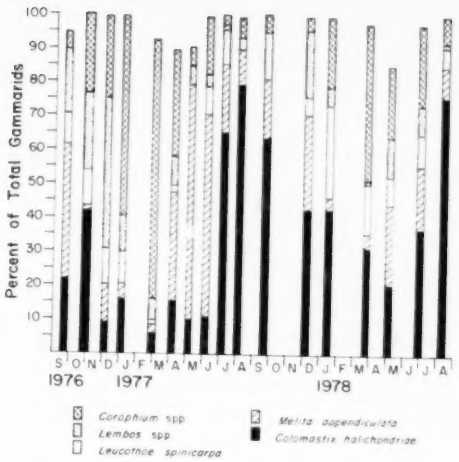

Fig. 9. Amphipod dominance in *Microciona prolifera*.

Differences between the amphipod faunas of *Halichondria bowerbanki* and *Microciona prolifera* are variable. However, it is clear that densities of *Colomastix halichondriae* are far greater in *Halichondria bowerbanki* and densities of *Corophium* spp. are somewhat lower. In fact, the specific name for *Colomastix halichondriae* is based on its common occurrence in this species of sponge. The total non-*Colomastix halichondriae* gammarid densities are very similar in both *Microciona prolifera* and *Halichondria bowerbanki* when based on sponge mass. *Halichondria bowerbanki* has a mean density of 0.076 g per cm³ (s = 0.012). This means that based on volume the densities of amphipods in *Microciona prolifera* and *Halichondria bowerbanki* are more similar. Based on the approximate volume of 5 g of *Microciona prolifera*, total gammarid densities in 40 cm³ of *Halichondria bowerbanki* for September 1976 through January 1977 are 218, 371, 307, and 312. Except for high densities in October, reference to Fig. 8 reveals that these are very similar to densities found in *Microciona prolifera*. On the basis of volume, densities of *Colomastix halichondriae* are still considerably greater and *Corophium* spp. somewhat lower in *Halichondria bowerbanki*.

TABLE 2. Number of individuals of major amphipod taxa in 5 g of sponge.

Taxa	1976			1977						1978	
	Sep	Oct	Dec	Jan	Feb	Apr	May	Jul	Aug	Dec	Jan	Jun
Lissodendoryx isodictyalis												
Colomastix halichondriae				3.4		0		72.8	92.5			
Leucothoe spinicarpa				13.0		0		81.6	190.6			
Melita appendiculata				4.4		8.4		25.8	20.5			
Corophium spp.				7.2		2.1		2.3	0.4			
Lembos spp.				32.9		0.6		3.8	0			
Total Gammarids				61.7		16.5		187.4	305.5			
Haliclona loosanoffi												
Colomastix halichondriae		53.8		12.7	1.0		49.2			85.4	36.0	81.2
Leucothoe spinicarpa		16.9		1.6	0		11.3			45.8	7.6	39.9
Melita appendiculata		4.3		0.8	0.2		50.8			4.2	0	6.7
Corophium spp.		7.4		24.6	5.5		33.2			108.3	12.1	17.8
Lembos spp.		31.4		32.2	3.4		24.8			572.9	4.2	2.3
Total Gammarids		115.3		76.3	12.4		257.1			825.0	60.2	148.3
Halichondria bowerbanki												
Colomastix halichondriae	323.9	1,563.8	303.0	483.5								
Leucothoe spinicarpa	27.8	87.9	29.5	79.1								
Melita appendiculata	94.9	46.6	27.8	15.8								
Corophium spp.	5.7	34.5	37.7	74.6								
Lembos spp.	16.8	119.0	85.4	36.1								
Total Gammarids	483.0	1,860.3	487.7	694.9								

TABLE 3. Probability (two-tailed Student's t-test) that the ratio of standard deviation:mean are the same for two species. The ratio is calculated using percentage of gammarid fauna for each sponge sample involving 3 or more individual sponges (8 samples of *M. prolifera* and 1 each of *L. isodictyalis* and *H. loosanoffi*).

	Leucothoe spinicarpa	*Colomastix halichondriae*	*Melita appendiculata*	*Corophium simile*
Colomastix halichondriae	.340			
Melita appendiculata	.015	.002		
Corophium simile	.055	.011	.831	
Lembos cf *L. websteri*	.001	.001	.005	.017

Haliclona loosanoffi was the most morphologically heterogeneous species sampled and this heterogeneity may be reflected in faunal variations. Samples taken in October 1976, May and December 1977, and January and June 1978, included sponges that had a very rough surface with upraised tubular projections and chimneys. Those collected in January, February, and May 1977 included specimens that were rounded and smooth surfaced, caused perhaps by the presence of large numbers of spionid mud tubes that were found on and in the sponge. Some of the sponges collected in February 1977 were dead or dying; this may have been responsible for reduced amphipod densities at that time. Densities of *Colomastix halichondriae* in *Haliclona loosanoffi* were, nevertheless, approximately the same as in *Microciona prolifera*, with the same seasonal trends evident. *Melita appendiculata* also shows the same seasonal trend as seen in *Microciona prolifera*, although densities and faunal percentages are generally lower than seen in *Microciona prolifera*. *Corophium* spp. shows the same seasonal trends in dominance found in *Microciona prolifera* (Fig. 9), although density differences are variable. Overall, *Haliclona loosanoffi* has lower amphipod densities than seen in *Microciona prolifera*, the exception being December 1977, when *Lembos* cf *L. websteri* occurred in unusually large numbers. *Haliclona loosanoffi* has approximately the same sponge density as *Lissodendoryx isodictyalis* (0.092 g per cm^3; s = 0.008). Therefore, as with *Lissodendoryx isodictyalis*, lower gammarid densities in *Haliclona loosanoffi* when compared with *Microciona prolifera* are even more pronounced when considering sponge volume.

As mentioned above, there was frequently considerable variation in amphipod densities between sponges of the same species collected at the same time. Two questions were therefore posed: 1) How do the major amphipod species compare with respect to the consistency of their density or faunal percentage in con-specific sponges at the same time; 2) Are there differences in amphipod densities between sponges of differing sizes? In order to answer the first question, the ratio standard deviation:mean was calculated for each of the five major amphipod species for each sampling date that included three or more sponge samples per species of sponge. This value was calculated for each species of sponge separately and was done for both density and faunal percentage. The lower the value of this ratio, the less variable are the densities or faunal percentages for that amphipod species in that sponge species on that date. In calculating densities, n + 1 counts for each sample were used to avoid the presence of zero values. Student's t-tests (two-tailed) were then done to compare the ratios for all pairs of these five species, the resultant probability matrix using faunal percentages shown in Table 3. *Leucothoe spinicarpa* and *Colomastix halichondriae*, the only two species that are largely obligate symbionts, display a significantly more consistent faunal percentage each sampling date than did the other three species. *Lembos* cf *L. websteri* was significantly less consistent in its faunal percentages than were the other four species. Although faunal consistencies showed the same relationships when considering density (*Colomastix halichondriae*, *Leucothoe spinicarpa* > *Melita appendiculata*, *Corophium simile* > *Lembos* cf *L. websteri*), there were no differences significant at the 90% confidence level.

To analyze the effect of *Microciona prolifera* colony size on faunal densites, densities (n + 1 values) of *Colomastix halichondriae*, *Leucothoe spinicarpa*, *Cor-*

TABLE 4. Values for the linear regression equation $Y = a + bX$, where Y is the $\log_{10}$ of the number of amphipods in 5 g of *Microciona prolifera* (n + 1 counts used) and X is sponge mass (g). See text for explanation of warm and cold seasons. Two-tailed Student's t-tests used for calculation of probabilities.

	a	b	r^2	Prob. $\beta = 0$
Leucothoe spinicarpa				
Warm	1.710	−0.163	0.299	0.108×10^{-3}
Cold	1.846	−0.197	0.701	0.295×10^{-3}
Total	1.754	−0.182	0.385	0.001×10^{-4}
Corophium simile				
Warm	1.432	−0.092	0.027	0.212
Cold	1.574	−0.149	0.220	0.068
Total	1.587	−0.147	0.098	0.662×10^{-2}
Colomastix halichondriae				
Warm	2.544	−0.174	0.304	0.096×10^{-3}
Cold	1.896	−0.057	0.042	0.431
Total	2.128	−0.071	0.038	0.087
Total gammarids				
Warm	2.635	−0.112	0.160	0.358×10^{-2}
Cold	2.248	0.006	0.001	0.909
Total	2.473	−0.056	0.049	0.057

ophium simile, and total gammarids in 5 g of sponge were calculated for each species in each sponge collected after July 1977. An estimation of the following linear regression equation was then made for each species:

$$Y = a + bX,$$

where Y is the log of the number of amphipods in 5 g of sponge and X is sponge mass (g). Linear regression analyses were done for all *Microciona prolifera* samples collected after July 1977, for warm season samples (June, August, September), and cold season samples (December, January, March). Results of these regression analyses (Table 4) demonstrate that except for *Corophium simile* in summer and *Colomastix halichondriae* and total gammarids in winter, there is a significant decrease in faunal density as the size of the sponge increases. Relatively low values for the coefficient of determination (r^2) indicates, however, that the relationship between log amphipod density and sponge mass is not linear.

Discussion

Although differences in amphipod densities were found between the four species of sponge studied, there is a general seasonal trend in amphipod dominance that holds in most cases. Winter dominance by *Corophium* spp. and on occasion *Lembos* spp. is followed by spring dominance by *Melita appendiculata* and summer dominance by *Colomastix halichondriae*. There were noticeable differences between the first and second years of this study concerning faunal densities, but less so with respect to faunal percentages (Fig. 9). The more severe cold conditions during the first winter may have been responsible for lower population densities of *Colomastix halichondriae* and *Leucothoe spinicarpa* and higher densities of *Lembos* spp. and *Corophium* spp. at that time, although temperature tolerance experiments and research on the population dynamics of these species would be needed to confirm this. As mentioned above, this winter did have a more severe effect on the sponges themselves than did the following winter. Significantly higher summer 1977 population densities of *Colomastix halichondriae* and *Melita appendiculata* when compared to summer 1978 are less easily explained. It could simply be a natural variation in population densities due to differences in fecundity, food, predation, etc. or it may be that since the number of available host sponges was less in the summer of 1977 than in the summer of 1978, the number of amphipods per

sponge was greater in summer 1977. Since the sizes of *Microciona prolifera* colonies collected in July 1977 were greater than those of June or August 1978, higher densities in July 1977 cannot be attributed to a presence of smaller colonies.

Densities of amphipods found in this study are considerably higher than those found in most prior investigations. Frith (1976) found a maximum total amphipod density of approximately 10 per 40 cm^3 in two species of sponge, with most other species showing far lower values. He found highest densities in the most cavitied sponges. *Halichondria bowerbanki*, a highly branched and somewhat cavitied species, generally did have the highest densities in the present study. However, *Lissodendoryx isodictyalis* and *Haliclona loosanoffi*, which are non-branching, usually rough or cavitied sponges, had lower densities than the smoother surfaced, long lobed *Microciona prolifera*. If, as suspected by Pearse (1932), there is a relationship between amphipod density and sponge surface area, high densities in *Microciona prolifera* may be due to higher surface area-to-volume ratios in this highly branched species. Also of possible importance may be certain chemicals found within sponges. *Lissodendoryx isodictyalis* has a characteristic strong garlic odor, perhaps indicating the presence of a chemical that inhibits colonization by spongicolous species (see De Laubenfels 1947). De Laubenfels (1947) collected over 89 amphipods per 40 cm^3 in North Carolina specimens of *Lissodendoryx isodictyalis*, a value that fits well within the range of results of this study. Pearse (1932, 1950) found that amphipods were very rare in the decapod-dominated loggerhead sponges he studied (up to 0.02 per 40 cm^3 for *Leucothoe spinicarpa* and up to 0.04 per 40 cm^3 for *Colomastix pusilla*). The largest number of amphipods collected from a single sponge by Pearse (1932) was 75 in a 50,000 cm^3-loggerhead sponge. In the present study the largest number of amphipods collected from a single colony of *Microciona prolifera* was 351 in a 5.1 g (41 cm^3)-colony. The largest number collected in any single sponge was 397 in a 2.4 g (26 cm^3)-colony of *Haliclona loosanoffi*. Unfortunately, Frith (1976) does not record amphipod totals for individual amphipod-dominated sponges that he studied. However, as mentioned above, the largest average density recorded was 10 amphipods in 40 cm^3 of two sponge species, compared with a maximum average density in the present study of 1,131 per 40 cm^3 in an October 1976 multicolony sample of *Halichondria bowerbanki*. Major amphipod species in Frith's British study were *Microdeutopus damnoniensis* (Bate), *Microdeutopus anomalus* (Rathke), and *Corophium sextoni* Crawford. No species of *Colomastix* or *Leucothoe* were recorded. *Colomastix halichondriae* is a very small species only 2–3 mm in length (Bousfield 1973), permitting large numbers to occur in relatively small amounts of sponge. Results of the present study agree with Frith's (1976) finding that no amphipod species were sponge-specific. Only variations in densities occurred between sponge species.

The finding in the present study that amphipod density generally decreases with increasing sponge size may also be true for loggerhead sponges (Pearse 1932). Since most sponge-inhabiting animals associate with the surface of the sponge, Pearse believed that this trend was probably the result of the inverse relationship of the sponge surface area to its volume. It is at least possible, however, that in some cases rapid sponge growth combined with both relatively low amphipod reproduction (relative to sponge growth) and emigration could result in decreased amphipod densities as their live habitat increases in size. This could explain why total amphipod density does not decrease in larger sponges in winter (Table 4), a time when the rate of sponge growth is probably minimal. Further studies on rates of sponge growth and spongicolous amphipod population dynamics are necessary before this possibility can be completely discounted.

That *Colomastix halichondriae* and *Leucothoe spinicarpa* are more consistent than *Melita appendiculata*, *Lembos* cf *L. websteri*, and *Corophium simile* in their proportion of the amphipod fauna found at any one particular time may be because a different relationship exists between these two species and their sponge host. *Colomastix halichondriae* and *Leucothoe spinicarpa* are the only two obligate sponge inquiline

amphipod species found in these sponges. It is possible that these two species have a greater dependence on the sponge than do the other more opportunistic species, perhaps due to feeding on sponge tissue. *Colomastix halichondriae* and *Leucothoe spinicarpa* could then be more sensitive to changes in sponge volume (or mass) or number of cohabitants relative to their population size than would the other species, resulting in greater consistency in their occurrences.

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